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The distribution and impact of an invasive plant species (*Senecio inaequidens*) on a dune building engineer (*Calamagrostis arenaria*)

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Abstract

Disturbance is thought to enhance the probability of invasive species establishment, a prerequisite for naturalisation. Coastal dunes are characterised by disturbance in the form of sand dynamics. We studied the effect of this disturbance on the establishment and spread of an invasive plant species (*Senecio inaequidens*) in European coastal dunes. Local sand dynamics dictate the spatial configuration of marram grass (*Calamagrostis arenaria*). Therefore, marram grass configuration was used as a reliable proxy for disturbance. Since marram grass plays a crucial role in natural dune formation, we evaluated the possible effects *S. inaequidens* could have on this process, if it is able to naturalise in European coastal dunes.

We expected the highest probability of *S. inaequidens* establishment at intermediate marram grass cover because too low cover would increase sand burial, whereas high cover would increase competition. However, our results indicate that *S. inaequidens* is quite capable of handling higher levels of sand burial. Thus, the probability of *S. inaequidens* establishment was high under low marram cover but slightly lowered when marram cover was high, hinting at the importance of competition.

We expected a negative impact of *Senecio*-altered soils on marram grass growth mediated by soil biota. However, marram grass grew better in sand gathered underneath *Senecio* plants due to abiotic soil modifications. This enhanced growth may be caused by *Senecio* leaf litter elevating nutrient concentrations in an otherwise nutrient-poor substrate. If such increased plant growth is a general phenomenon, further expansion of *S. inaequidens* could accelerate natural succession in European coastal dunes.

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Keywords
Ammophila arenaria, disturbance, Marram grass, Narrow-leaved ragwort, naturalization, plant-soil feedback, pyrrolizidine alkaloids, South African ragwort

Introduction

Due to human activity the number of invasive species worldwide is ever-increasing. In Europe alone, the number was estimated to be well over 12 000 in 2019 (Roy et al. 2019). The causes of introduction of non-native species range from intentional introduction, e.g., for pest control, horticulture, coastal defence and restoration purposes (Cox 1992; Beckstead and Parker 2003; Richardson and Rejmánek 2011; Camacho-Cervantes et al. 2017; Buerdsell et al. 2021) to unintentional introduction such as escape from planting sites and introduction via tourism (Davenport and Davenport 2006).

After reaching a new habitat, the non-native species needs to establish and naturalize in order to become invasive (Richardson et al. 2000). It is generally thought that disturbance benefits establishment of non-native species and that it could even facilitate the spread of invasive species. Several mechanisms, such as reduced competition, increased resource input and increased habitat availability, are proposed to be behind this phenomenon (Mack et al. 2000; Pyšek and Richardson 2006; Jauni et al. 2015; Lear et al. 2020).

Several hypotheses have been proposed to explain the long-term success of invasive species (Mack et al. 2000; Chabrerie et al. 2019). Among these, the enemy release hypothesis (**ERH**) and the Evolution of Increased Competitive Ability hypothesis (**EICA**) are particularly important in the context of harsh, temporally variable environments in which biotic interactions can be hampered. The ERH states that the success of invasive species can be attributed to the release from natural enemies such as (specialized) herbivores or pathogens (Keane and Crawley 2002). The EICA adds to this that, due to the release from natural enemies, invasive plant species can reallocate resources otherwise used for protection towards growth and other performance traits (Blossey and Notzold 1995).

Invasion can also be promoted via both intra- and interspecific facilitation (Jordan et al. 2008; Proença et al. 2019; Uyà et al. 2020), especially in harsh environments, or by decreasing fitness of native species (Jordan et al. 2008; Vilà et al. 2011). One underlying mechanism in plant communities is modification of the soil (Aldorfová et al. 2020). The effect of such modifications can be very useful because invasive species can provoke generic effects against the whole native community, which enables them to invade if they suffer less from their created disaster. Contrastingly, it is hard for the native community to specifically target a newly arrived, invasive species (David et al. 2017). The term 'plant-soil feedback' (PSF) refers to the process of plants altering the soil with effects on the performance of other plants subsequently growing in this soil (Bever et al. 1997; van de Voorde et al. 2011; Buerdsell et al. 2021). The soil characteristics altered can be biological, chemical or structural (Ehrenfeld et al. 2005; Kulmatiski et al. 2008). Biological modification of the soil occurs via changes in the soil community, including soil microbes and soil fauna. Depending on the affected species, these

effects can be negative, e.g., when root-feeding nematodes or pathogens accumulate (Van der Stoel et al. 2002; Bever et al. 2015) or mutualistic interactions are disrupted by the non-native plant (Callaway et al. 2008; Brouwer et al. 2015), or positive, e.g., by accumulation of mycorrhizal fungi or nitrogen-fixing bacteria in low-nutrient soils (Rodríguez-Echeverría et al. 2009; in 't Zandt et al. 2019). Root exudates, litter decomposition and root-supported microbial activity can alter different components of the soil chemistry such as soil acidity and nutrient availability (e.g., Lazzaro et al. 2014). Structural modification occurs via changes in soil temperature, water content or the overall soil structure and soil aggregates (Ehrenfeld et al. 2005). Again, these effects can be either negative or positive, depending on the species (Bezemer et al. 2006).

Plant-soil interactions can affect the process of species invasion at different scales. Plant-soil interactions are local and thus mainly affect the plant itself or other plants in the near vicinity, both conspecifics and heterospecifics. Invasive tree species can, however, have more wide-ranging effects using their fallen leaves as agents of soil change (e.g. Gómez-Aparicio and Canham 2008). At larger spatial scales, different local plant-soil interactions give rise to a heterogeneous, spatially structured landscape (Bever et al. 1997; Mack and Bever 2014) which influences biodiversity, population dynamics and ecosystem functioning (Levine et al. 2003; Vilà et al. 2011; Mack and Bever 2014). This heterogeneity can, in turn, influence the processes facilitating species invasions, such as enemy release or fitness decrease in native competitors.

European marram grass (*Calamagrostis arenaria* (L.) Roth, formerly *Ammophila arenaria*) is one of the most extensively studied systems regarding PSF, with studies investigating abiotic and biotic PSFs going back to the 60s (Marshall 1965) and 80s (Van der Putten et al. 1988) respectively. This study focuses on marram dunes (Natura 2000 habitat 2120, CORINE biotope 16.21), a coastal habitat type dominated by marram grass, which occurs relatively early in the dune succession, characterised by high levels of stress (Kulmatiski et al. 2008) due to e.g. sea spray and aeolian sand burial (Brown et al. 2018). Marram grass is perfectly adapted to grow in these conditions. Several studies have shown that marram grass even needs sand burial to grow optimally (i.e. Nolet et al. 2018; Ievinsh and Andersone-Ozola 2021) because the biological soil community accumulating around the roots of marram grass has a negative impact on its performance and growth (Van der Putten et al. 1988; Van der Stoel et al. 2002). Deposits of sand blown in from the beach are relatively free of root pathogens and parasites and thus enable marram grass to develop new roots in this temporarily enemy-free soil. Additionally, marram grass also interacts with the aeolian sand dynamics by locally lowering the wind speed and thus promoting sand capture (Zarnetske et al. 2012; Reijers et al. 2021), resulting in a positive feedback between marram growth and sand capture. This interplay between marram grass and sand dynamics leads to a range of possible spatial configurations of marram grass, which depend on the local sand dynamics. Reijers et al. (2021) found that marram grass grows highly clustered together under sediment-poor conditions. When there is enough sediment supply, it grows more randomly, albeit still clustered (Reijers et al. 2021). This allows marram grass cover to be used as a proxy for the intensity of sand dynamics. Marram grass can reach a high density when enough fresh sand is provided by strong sand dynamics.

Under moderate sand dynamics, an optimal spatial configuration is expected to occur with a heterogeneous mosaic of bare sand and marram grass. Since this species grows via lateral vegetative growth, natural configurations show variable degrees of clustering, but rarely occur in truly random, let alone regular configurations.

The bare sand patches between marram grass tussocks may provide an opportunity for invasive species to establish. On the other hand, too dynamic conditions will probably hinder settlement due to too high levels of sand burial (Maun 1998; Kent et al. 2005). These conflicting pressures could determine where invasive species are able to establish in marram-dominated dunes. If these sand patches become overgrown, sand dynamics can further decrease (Gao et al. 2020) and in turn this can negatively affect the vitality of marram grass. This could lead to the invasive species becoming competitively stronger and outcompeting marram grass (i.e., a form of positive density dependence). Such changes in competition could have extensive consequences for coastal dunes and their ecosystem services (Klironomos 2002), especially coastal defence, as they could trigger feedbacks that change system dynamics (Bonte et al. 2021).

One species invading coastal dunes around the North Sea is narrow-leaved ragwort (*Senecio inaequidens* D.C., Asteraceae, also known as South African ragwort). It is originally a South African species, but with a long history of invasion in Europe (Ernst 1998), where it arrived via wool transport (Lachmuth et al. 2010). Although much is known about the invasion of *S. inaequidens* in other habitats in Europe (Ernst 1998), far less is known about its colonisation of sandy dune areas. It was first found in dune areas in 1935, more specifically in the dunes of Calais, France (López-García and Maillet 2005).

Senecio species contain pyrrolizidine alkaloids (PA) as a defence mechanism against both above- and belowground herbivory (Joshi and Vrieling 2005; Caño et al. 2009; Thoden et al. 2009; Joosten and Van Veen 2011). Several studies have shown these allelopathic defences can influence entire soil communities (Kowalchuk et al. 2006; Thébault et al. 2010; Harkes et al. 2017) and therefore *Senecio* species are able to affect their own spread (Engelkes et al. 2008). However, the exact mechanisms are, to our knowledge, still unknown. Passive release from roots (and leaf litter) is the most probable pathway, although it is speculated that direct secretion from the roots is possible as well (Kowalchuk et al. 2006; Joosten and van Veen 2012; Selmar et al. 2019). Not many studies have tried to investigate the direct effect of PAs on plant growth (but see Ahmed and Wardle 1994). Recently, even uptake of PAs by other plant species was demonstrated (Nowak et al. 2016; Selmar et al. 2019), although the general consequences of this horizontal transfer for the receiving plants are unknown at the moment.

We suspect that PAs in sandy soil will have little effect on marram grass growth directly. The sign of the total effect of *S. inaequidens* will depend on the response of the soil community. It will be negative if marram pathogens can accumulate or if PAs prevent symbionts from associating with marram roots. However, it can be positive if PAs prevent accumulation of marram pathogens and thus create an enemy-free space for marram roots, as aeolian sand does.

Here, we investigate the relation between marram grass spatial configuration and the probability of establishment of *Senecio inaequidens* in marram dunes, together with the potential effects of this invasion on marram dunes. We hypothesize that (1) due to

the potentially positive effect of disturbance on invasive species (Scherber et al. 2003; Jauni et al. 2015), *S. inaequidens* will likely get established in more disturbed areas, i.e. areas with stronger sand dynamics. However, since too high sand burial is probably detrimental for the growth of *S. inaequidens*, we expect to find an optimum at intermediate sand burial which is also associated with intermediate vegetation cover. We further postulate that (2) the biotic compartments of *Senecio*-altered soils will negatively affect marram grass growth, except if PAs prevent marram pathogens from accumulating.

Material and methods

Study area

This study was carried out in coastal dune areas along the Channel and the North Sea, covering the North of France, Belgium, the United Kingdom and the Netherlands (Fig. 1). Within this area, we focussed on sandy coasts with marram-dominated, yellow dunes. This area included the location of *S. inaequidens* settlement and the northernmost location within its distribution in coastal dunes, thus enabling us to study the front of the ongoing invasion.

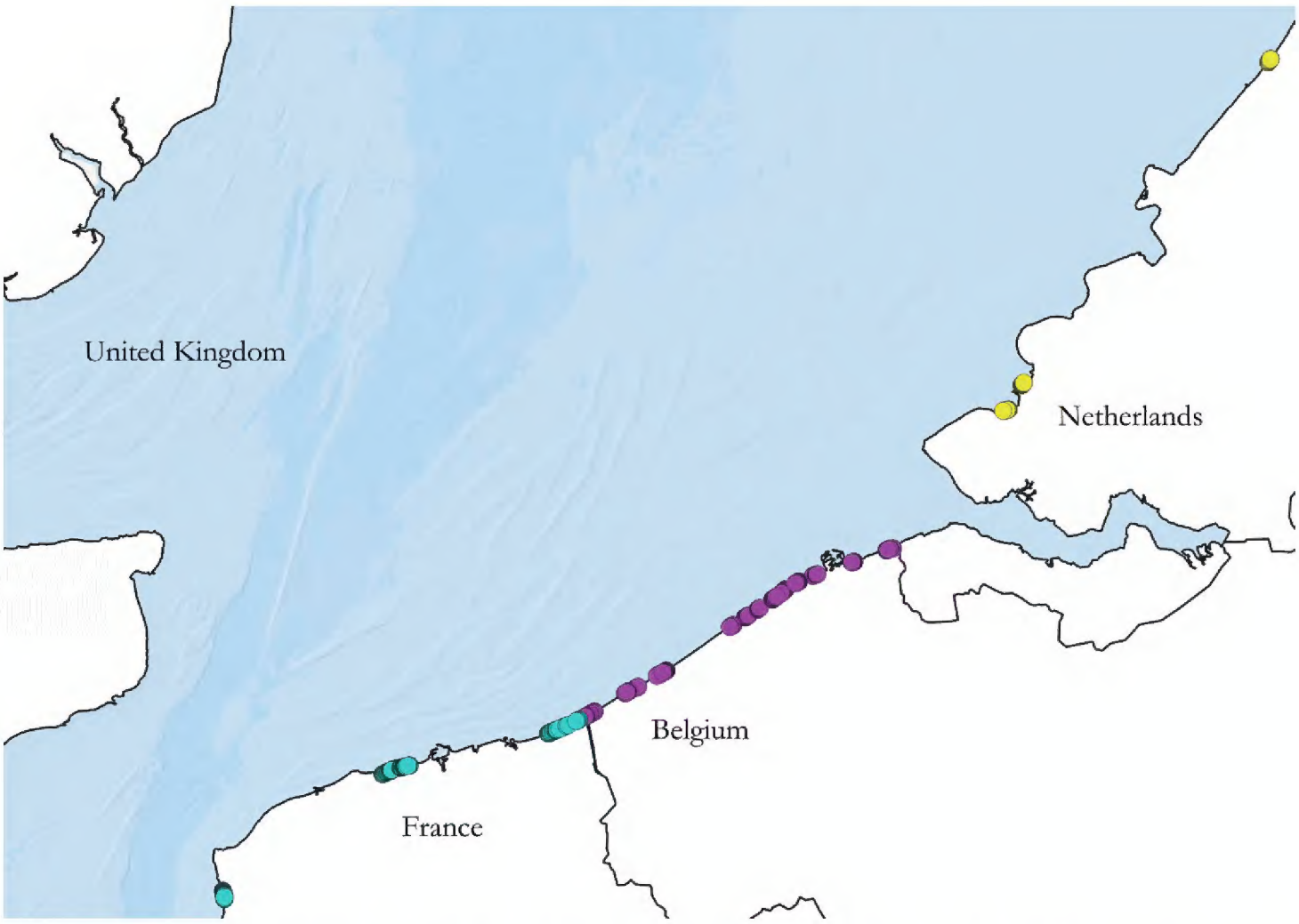

Figure 1. The samples included in the analysis. Colours indicate the different countries. *Senecio inaequidens* was not found in the UK. Map made with QGIS v3.6 (QGIS Development Team 2021).

For a recent biodiversity study, 46 dune transects spread along the study area were selected. The transects had a mean length of 1212 m (shortest: 230 m, longest: 3348 m) and were located within the first 100 m from the front of the foredunes. Within each transect a number of sampling locations was chosen based on the length of the dune transect with an average of 14 samples (min 5; max 37). Each sampling location was characterized by a central marram grass tussock. Individual sampling locations were separated by at least 20 m and chosen with the aim to maximise the variety of surrounding marram grass configurations. For the total number of samples and transects per country, see Table 1.

Table 1. The number of samples taken in each country within the study region.

Country	Samples	Transects	Mean length of transects
BE	206	18	822
FR	184	9	2232
NL	188	13	800
UK	60	6	720

Data collection

The occurrence of narrow-leaved ragwort (*Senecio inaequidens*) was mapped at each sampling location. The number of *S. inaequidens* plants was counted within a radius of 5 m around the central marram grass tussock for those sampled in France, the UK and the Netherlands. Due to a change in the protocol of the biodiversity study, in Belgium the occurrence was scored into four categories: "not present", "sparse", "moderate" and "abundant". Data on the occurrence of *S. inaequidens* were collected during three consecutive summers: in July 2017 data were collected along the Belgian coast; in July, August and September 2018 along the French coast; in August and September 2018 and June 2019 along the Dutch coast; and in July and August 2019 along the coast of the UK (Norfolk and Devon).

From available vegetation maps of the foredunes (Bonte et al. 2021), the proportional cover by marram grass in the vicinity of the central marram grass tussock (P), together with a measure of spatial autocorrelation of marram grass occurrence (normalised join count statistics, JC; Cliff and Ord 1981), were calculated. These two parameters were used to express the spatial configuration of the surrounding marram grass. The proportion of marram grass cover is straightforward and ranges from 0 (no marram grass present) to 1 (the whole area is covered with marram). The measure of spatial autocorrelation is negative when the marram grass is regularly distributed in the landscape. If the marram grass is randomly distributed, the parameter is close to 0 and it is positive when the marram grass occurs clustered together. As pointed out by Bonte et al. (2021), marram grass distribution is almost always clustered (i.e., high JC values) and rarely random. These two parameters (P and JC) were calculated within four circles with different radii (5 m, 10 m, 20 m, 50 m) around the central marram

grass tussock to represent different spatial scales. See supplementary material of Bonte et al. (2021) for a more in-depth explanation of construction of the vegetation maps and calculations of the spatial parameters.

Lab experiment

To study the effect of *S. inaequidens* on marram grass growth, we performed a growth experiment with a split-plot design: sand affected by *S. inaequidens* was gathered at the Belgian coast together with bare sand for the control group. Half of the volume of sand gathered was sterilised (by autoclaving at 121 °C/1 bar for 30 minutes) in both groups to determine whether any observed effect could be biotic or abiotic.

Sand was gathered from three different sites situated on the western, central and eastern Belgian coast: in the foredunes in Oostduinkerke (Ter Yde) for the west coast, for the mid coast in Oostende (Fort Napoleon) and for the east coast between Wenduine and Zeebrugge (two locations were used due to low occurrence of *S. inaequidens*). Ten plots were sampled at each site (for a total of 30 plots). Each plot yielded two samples: 2L rhizospheric sand from underneath *S. inaequidens* plants and 2L of bare sand taken 5–10 m away. This way, changes in soil between two paired samples, other than due to the influence of *S. inaequidens*, were minimised. The sand was stored in the fridge (max 3 days) to assure the survival of the soil biota until the sand was used. The 2L samples were divided into two 1L sub-samples from which one was sterilised and the other was not. Thus, we had four treatments: *Senecio*-influenced vs. bare sand at the plot level combined with sterile vs. non-sterile soil at the subplot level (Fig. 2). In other words, influence of *Senecio* was the whole-plot factor and soil sterilisation the subplot factor, with whole plots organized in pairs, which act as statistical blocks.

Marram grass seedlings were used for the experiment because seedlings are more susceptible to environmental influences than fully grown plants (Huiskes 1979). The seedlings were grown from seeds gathered at the Belgian coast (Oostduinkerke, ter Yde) from the same population in order to minimize genetic effects. The seeds were collected during the summer of 2019 and stored at room temperature in the lab. All seeds were surface-sterilised as in de la Peña et al. (2010) before they were left to germinate under standardized conditions (on commercially available sand saturated with demineralized water; photoperiod: 16/8 h light/dark; temperature: 22 ± 1 °C) for 2 weeks prior to dune sand collection. As a baseline, the whole seedlings were weighed and the length of roots and leaves was measured before planting.

All 120 pots (3 sites × 4 treatment combinations × 10 plots) were filled with 1L of sand in which three seedlings were planted. The pots were placed in a growing chamber under the same conditions as mentioned before for the germination of the seeds. All pots were watered twice a week, on the same day, with demineralised water until near-saturation. Each pot was labelled with a unique ID in order to prevent observer bias.

After 2 weeks of growing, the largest seedling was selected to grow for another 10 weeks. The other two seedlings were removed. This was done to ensure that all remaining seedlings had rooted properly in order to minimise die-off and resulted in only

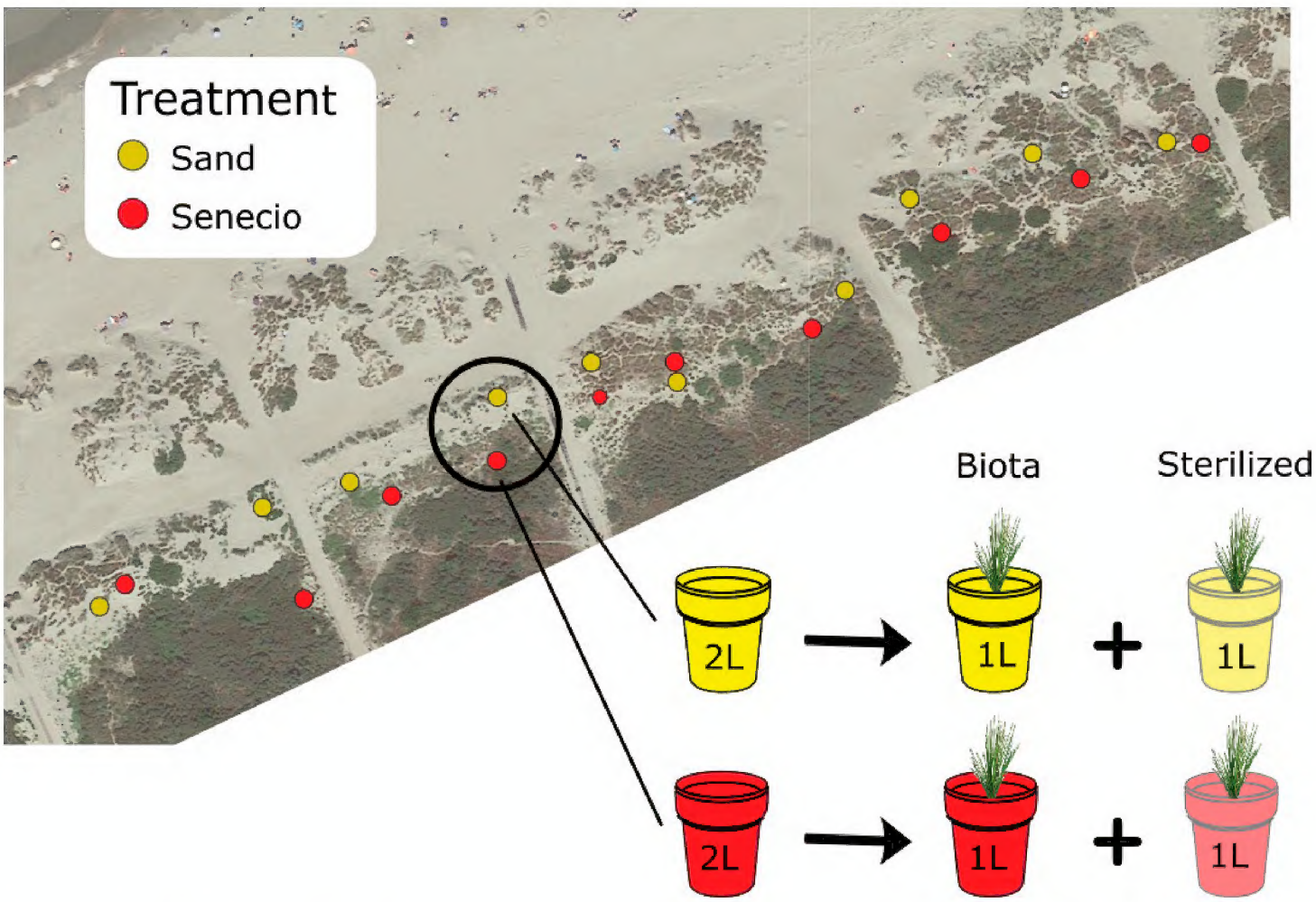

Figure 2. Split-plot design of the growth experiment for the site at Oostduinkerke (Western Belgian coast). 2L samples of sand, (1) sand from unvegetated locations or (2) sand from underneath *Senecio*, were split into two 1L subsamples, one of which was sterilized. This enabled us to investigate whether the effect of *Senecio* was achieved via the biotic or abiotic portion of the soil. Map made with QGIS v3.6 (QGIS Development Team 2021). Aerial photograph (summer 2018) source: Agency for Information Flanders (geopunt.be).

three plants dying during the whole experiment (one from each treatment, except for the sterilized bare sand treatment). At the end of the growing period the whole plants were collected, all leaves were counted and the length of the longest leaf and root was measured. Further, all leaves and roots were weighed separately, both before and after drying in an oven at 70 °C for 48 h.

Statistical analyses

Occurrence of *Senecio*

Due to two different methods of assessment of the occurrence of *Senecio inaequidens* (i.e. ordinal categories for the Belgian samples and count data for all other samples), all *S. inaequidens* data were converted to presence/absence. To exclude false zeros (i.e., samples along dune sites where *S. inaequidens* is not yet established) from the analysis, only dune transects where *S. inaequidens* occurred in at least one sample were included. This resulted in a final dataset comprising 26 out of the 46 original sites, which included 408 of the original 638 samples. The sites were located in three countries since *S. inaequidens* was not observed in the United Kingdom.

The marram grass spatial data were used as independent variables. As explained above, the spatial data consisted of two continuous variables: the proportion of marram grass (P) and its normalized join count statistic (JC) for each spatial scale (5 m, 10 m, 20 m and 50 m) per sample. The JC values were rescaled to the maximum value to alleviate convergence issues of linear models. This resulted in both parameters ranging between 0 and 1. Generalised linear mixed models were used with a logit link function and binomial distribution to analyse the occurrence data. A combination of first and second order terms of P and JC, together with interactions between them, were fitted to allow the relationship between the occurrence of *S. inaequidens* and the spatial parameters to be unimodal. The maximal (full) generalised linear mixed models were of the form:

$$\text{occurrence} \sim P + JC + (P \times JC) + JC^2 + P^2 + (P^2 \times JC) + (JC^2 \times P)$$

To determine which combination of P and JC best explained the occurrence data, different combinations of the spatial predictors were fitted (including interactions terms, see Suppl. material 1: Table S1 for all models) at all four scales (i.e. using P and JC computed at 5 m or 10 m or 20 m, etc.), after which model selection based on the corrected Akaike Information criterion (AICc) was used to select the model and scale that optimised goodness-of-fit. Dependency is present within the data for samples along the same transect. Therefore, 'transect' nested within 'country' was included in the models as a random variable. 'Country' itself was excluded because it contained almost no variation (Chen and Dunson 2003). This way we also accounted for differences in weather, dune management and time (different countries were sampled in different years).

Growth experiment

We analysed the effect of the provenance of the sand (from beneath *S. inaequidens* vs. bare sand), of its sterilisation and of their interaction using linear mixed models. F-tests with Satterthwaite's approximation of denominator degrees of freedom were used to determine the significance level of the fixed effects. All measured traits (number of leaves, length of longest leaf and root, weight of fresh and dry roots and leaves) where highly correlated (see Suppl. material 1: Fig. S1, Table S2), so we used the first principal component (PC1) from a principal component analysis run on the trait data as response variable for the analysis. Sample site and plot were integrated in the mixed model as random effects to account for data dependency within block and whole-plots. Sample was initially also included to correct for dependency of the subsamples within each sample, but this random effect was removed because of a negligible variance component.

All data analyses were performed using R Statistical Software (R Core Team 2021). The calculation and normalisation of JC values was done with the 'spdep' package (Bivand and Wong 2018). The packages 'lme4' (Bates et al. 2015) and 'lmerTest' (Kuznetsova et al. 2017) were used for the Generalized linear mixed models. Package 'MuMIn' (Barton 2020) was used for automated model construction and comparison.

Results

Occurrence

Senecio inaequidens was observed at 176 of the 408 sites included in the analysis. The most northern and southern transect where *S. inaequidens* was observed are respectively at Wassenaar (52.1565°N, 4.3404°E; the Netherlands) and Wimereux (50.7931°N, 1.6074°E; France). *S. inaequidens* was most frequently present in Belgian samples, followed by France and the Netherlands (Fig. 3). In the United Kingdom, no *S. inaequidens* was observed.

The four models selected were all at the 5 m scale (using an AICc delta value of 2; see Table 2 for the selected models; see Suppl. material 1: Table S1 for all models), implying that *S. inaequidens* reacts to marram grass spatial configuration at small distances. The predicted occurrence is depicted in Fig. 4a. When the vegetation is highly clustered together (high JC values), the occurrence of *S. inaequidens* is negatively correlated with marram grass cover. Further, we see a clear minimum probability of occurrence of

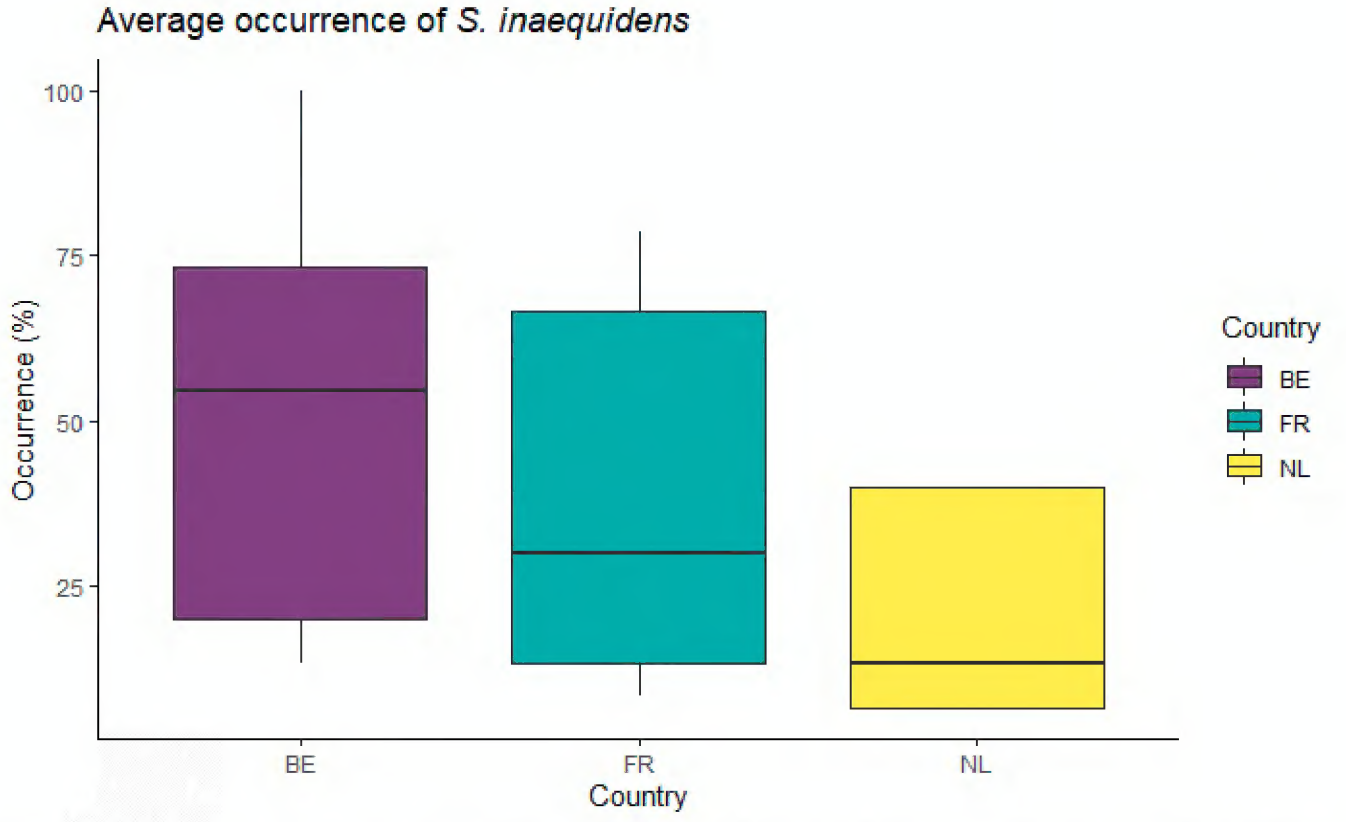

Figure 3. The average occurrence of *S. inaequidens*, calculated as the proportion of samples within each transect where *S. inaequidens* was found. BE = Belgium; FR = France, NL = the Netherlands.

Table 2. The coefficients, number of model parameters (df), AICc values, relative AICc (ΔAICc; i.e., difference between each model's AICc and the minimum AICc) and Akaike weights for all selected models.

Spat. scale	Intrcpt	JC	JC²	P	P²	JC*P	JC*P²	JC²*P	df	logLik	AICc	Δ AICc	weight
5	-1.4	6.13		-8.84	15.75		-13.71		6	-182.35	376.96	0	0.13
5	-2.53	15.39	-11.49	-24.36	28.00	23.84	-32.06		8	-180.9	378.24	1.285	0.068
5	-3.14	12.46	-5.35	-8.92	14.82		-12.19		7	-181.99	378.32	1.367	0.065
5	-0.12	3.94		-16	22.28	11.32	-23.80		7	-182	378.34	1.379	0.065
Avg.	**-1.73**	**8.88**	**-3.45**	**-13.50**	**19.40**	**7.20**	**-19.21**						

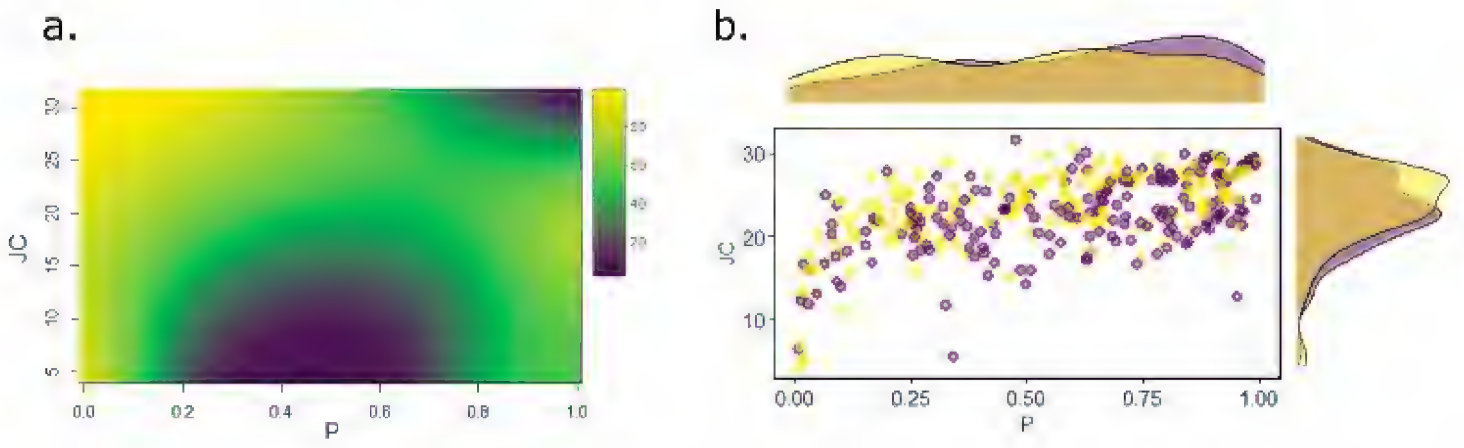

Figure 4. a The overall relation between the probability of occurrence of *S. inaequidens* and the spatial configuration of marram grass. The colours indicate the probability of occurrence as %. **b** Density distribution plots of the observed cover (P) and spatial autocorrelation (JC) of marram grass within a 5 m radius of the central marram grass tussock. This plot only contains the data of the transects where *S. inaequidens* was found. Colours indicate whether *S. inaequidens* was present (yellow) or absent (purple).

S. inaequidens at more random distributions of marram grass (low JC values) with intermediate vegetation cover. Since no random configurations were found at intermediate P, the minimum is probably due to a small number of samples with a low JC (see Fig. 4b), thus caution is advised when interpreting this result. Although we actively tried to sample in a wide range of different spatial configurations of marram grass, there is still a low number of data points with low marram grass cover and less clustered configurations due to the nature of the system. To ascertain that the outcome of the analysis was not greatly influenced by those few samples, the analysis was redone after excluding those samples. The results did not differ greatly (see Suppl. material 1: Fig. S2).

Growth experiment

The first PC of the PCA of all measured plant traits explained 73.9% of the variation, while the second PC explained 14.7%. Scores along PC1 were significantly correlated with all plant traits (see Suppl. material 1: Fig. S1, Table S2), therefore, we used PC1 as a reliable indicator of overall plant growth. Marram grass growth was affected by both the abiotic and biotic components of the soil (Fig. 5). However, no significant interaction was found ($F_{1,82.7} = 1.10$, $p = 0.298$). Soil sterilisation had a positive effect on marram growth ($F_{1,83.4} = 106$, $p < 0.001$), which means that the soil biota had a negative effect on marram biomass. The plants grown on sand from underneath *S. inaequidens* grew better than plants grown on bare sand ($F_{1,82.7} = 59.2$, $p < 0.001$).

Discussion

Field data

No evidence was found for the hypothesized optimum probability of establishment of *S. inaequidens* at intermediate marram grass densities. In fact, our results indicated that

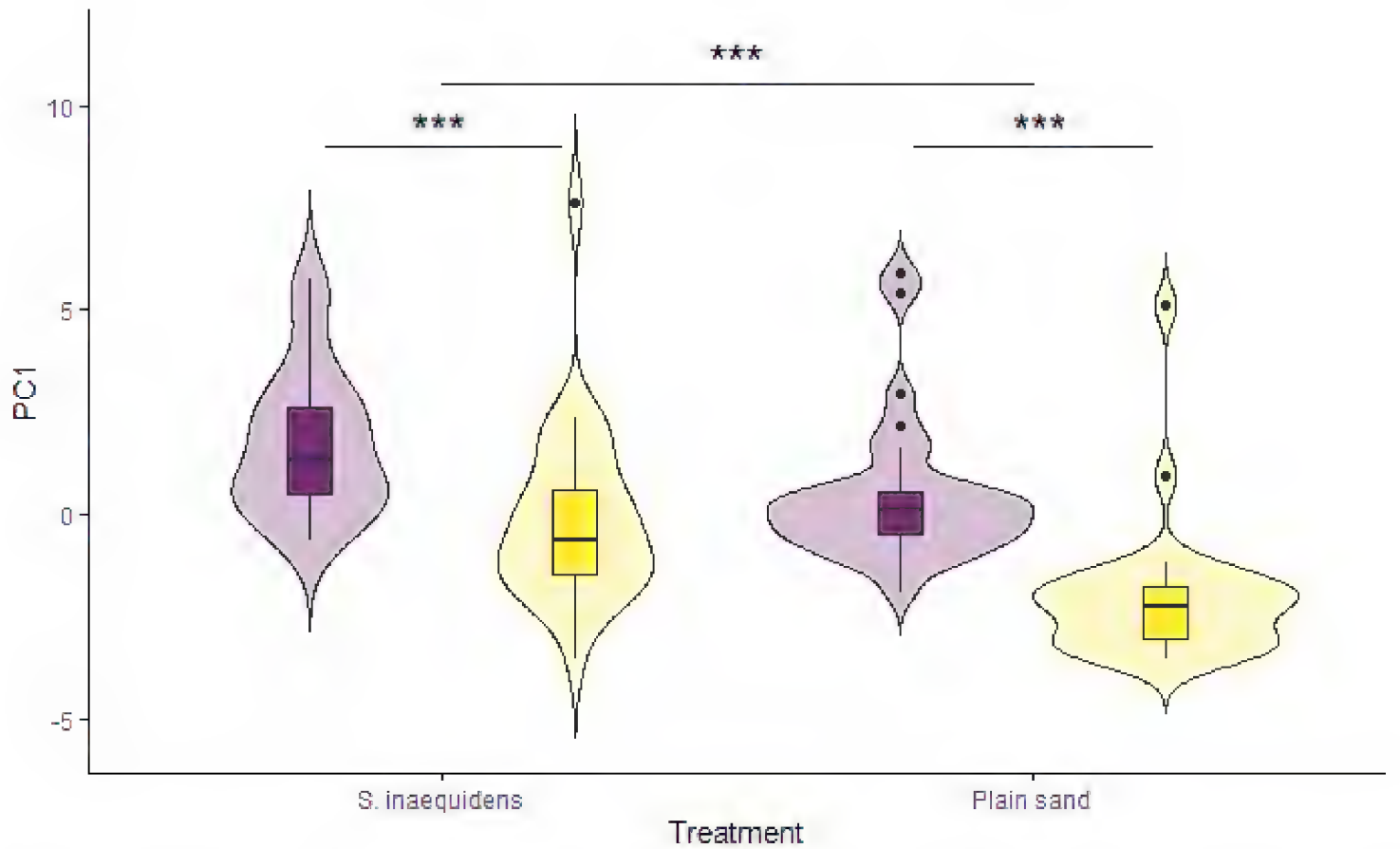

Figure 5. Box- and violin plots represent distribution of PC1 values for marram grass growth. Horizontal lines above the boxplots indicate comparisons between treatments, *** indicate significant difference of $p < 0.001$. Colours indicate whether biota were present (yellow) or absent (purple). Number of samples per treatment is 29, except for sterilized sand from unvegetated locations, where it is 30.

S. inaequidens has no problem growing in sandy conditions, as we observed a negative correlation between vegetation cover and probability of establishment. This indicates that *S. inaequidens* is more susceptible to competition than to sand burial. Indeed, some studies found that this species is a good coloniser rather than a good competitor (Scherber et al. 2003; Caño et al. 2007; Thébault et al. 2011). Furthermore, the available area to root in – in this case open sand – also decreases as vegetation cover increases. This is especially important since *S. inaequidens* is an annual plant which relies on high propagule pressure to spread (Thébault et al. 2011).

Due to the nature of the system, higher proportions of marram grass occur mainly towards later stages of succession. In these later stages, marram starts to decay and the spatial configuration starts to return to a more random distribution (i.e. lower JC values and slightly lower P values) because marram grass is slowly being replaced by other plant species. This leads to a rise of the probability of *Senecio* establishing which may indicate that it is becoming a stronger competitor.

Overall, the probability of establishment of *S. inaequidens* displays high values across the whole range of sampled natural marram grass configurations. Since we aimed to maximise the variety of natural marram grass configurations surrounding the sample, configurations that were not sampled probably do not, or not often, occur in nature. In fact, such configurations arise probably mainly when marram grass is planted (i.e., for coastal protection) and afterwards when the planted dune is 'maturing'. This makes it hard to extrapolate our findings to these specific situations.

Growth experiment

We hypothesised that the effect of *S. inaequidens* on marram grass growth would be negative, mainly because of interactions with the soil community. However, we concluded that the overall effect is positive. This effect is purely abiotic, since there is no significant interaction between sand sterilisation treatment and the provenance of the sand (underneath/away from *Senecio*). Similarly, intraspecific plant-soil feedbacks from *Senecio jacobaea* are also known to be (partly) abiotic (Wang et al. 2019), although the effect was negative in the cited study. Dassonville et al. (2008) showed that invasive species (*S. inaequidens* being one of the species included in their review) can have a positive effect on nutrient concentrations in plots with initially low concentrations. Since sand indeed has low nutrient concentrations (Reijers et al. 2020), this explanation is applicable here. Currently, we cannot verify this explanation since nutrient concentrations were not measured in the experiment.

Because marram grass growth was promoted in sand influenced by *S. inaequidens*, we can conclude that pyrrolizidine alkaloid concentrations had no, or a negligible, negative effect on marram grass. This is not surprising, since the most probable mechanism of PA enrichment of the soil is via passive release from roots and leaf litter (Joosten and van Veen 2012; Nowak et al. 2016; Selmar et al. 2019) and because some plants are even known to take up PAs without experiencing adverse effects (Nowak et al. 2016; Selmar et al. 2019). In contrast, Ahmed and Wardle (1994) found a negative effect of PA on plant growth. In our study, such a negative effect of PAs may have been counteracted by the simultaneous nutrient enrichment caused by *S. inaequidens*. This is in line with the observations by Reijers et al. (2020) that marram grass is more capable of coping with stressful conditions when nutrient availability is higher.

We observed a significant negative effect of soil biota on marram growth, with sterilisation of the soil having a positive effect on the biomass of marram, independent of the sand origin. This indicates that soil biota in the *Senecio* rhizosphere have approximately the same (negative) effect as the community within unvegetated sand. Thoden et al. (2009) found that PAs suppress the development of juvenile *Meloidogyne hapla* nematodes. Species from this genus also colonise marram grass. However, it was suggested before that nematodes from this genus do not develop to adults on marram grass anyway (Van der Stoel et al. 2002). On the other hand, *Pratylenchus* nematodes are able to colonise both *Senecio* (Zasada et al. 2017) and marram grass roots (Van der Stoel et al. 2002), which would enable infection of marram roots by *Pratylenchus* spp. present on *Senecio* roots. However, arbuscular mycorrhizal (AM) fungi have low levels of endemism and host specificity (Davison et al. 2015; Aldorfová et al. 2020) and are known to colonise roots of *Senecio* spp. (van de Voorde et al. 2010; Alguacil et al. 2012; Reidinger et al. 2012). Since both European and American marram grass (*Calamagrostis arenaria* and *C. breviligulata* resp.) benefit from AM fungi when faced with nematode infection (Little and Maun 1996; De La Peña et al. 2006), it is possible that the negative effect of the nematodes is counteracted by the AM fungi also accrued on the *Senecio* roots. Furthermore, some studies have shown that *Senecio* species effectively reduce density or diversity, depending on the study, of whole soil communities (Kowalchuk et al. 2006;

Thébault et al. 2010; Harkes et al. 2017). However, since these studies focussed on the effect on whole soil communities, it is difficult to make predictions for marram grass specifically. We conclude that PA concentrations in the field did not reduce the overall negative effect of the soil community, either because the community as a whole was affected and thus both negative and positive elements therein were reduced or because PA concentrations are too low to affect the soil community in general.

Our results indicate that the biotic soil community surrounding *Senecio* roots has approximately the same (negative) effect as the community within sand without plants growing in it (i.e., no significant interaction effect). Since endoparasites are known to be more damaging to marram grass (Van der Putten and Van Der Stoel 1998), it could be that we excluded their effect because we did not use an inoculum from *Senecio* to infest the soil and consequently marram roots with endoparasites. On the other hand, the biota accumulating on the senecio roots could not be compatible with marram grass roots at all. Consequently, sand from unvegetated patches, which is thought to function as a temporary 'enemy-free' space for marram grass to root in (Van der Stoel et al. 2002), has the same biological effect on marram growth as *Senecio*-influenced sand.

The observed positive effect of sterilisation in the unvegetated sand is caused by soil biota, such as nematodes, who have survival stages that can disperse in the dunes (e.g., *Heterodera* cysts) and subsequently colonise the marram grass roots in the lab (e.g., De Rooij-Van Der Goes 1995; Van der Stoel et al. 2002). Indeed, studies investigating marram grass PSFs frequently used sand from the beach or even the sea floor for their control treatment (Van der Putten et al. 1988; Van der Putten and Troelstra 1990). However, we decided to take sand from the foredunes in order to maximise similarity of soil characteristics between *Senecio*-affected and unvegetated paired samples.

Since we only studied correlations, it could be that *S. inaequidens* established only on the more nutrient-rich sand in the dunes, which would in turn explain why marram grass grows better in this sand. However, this is very unlikely since dunes are extremely dynamic and hence the top layers of sand are thoroughly mixed, creating a homogenously resource-poor environment (Reijers et al. 2020). Furthermore, marram grass was growing in the dunes long before *Senecio*, thus, if there would be patches with more nutrients, those patches would likely already have been occupied by marram grass. When sand is fixated by plant roots, the mixing is halted and nutrient heterogeneity can start to occur. Since we took sand from the rhizosphere of *S. inaequidens*, higher nutrient availability caused by *S. inaequidens* is still a viable explanation for our findings.

Integration of field data and experiment

Sandy habitats, such as coastal dunes, are characterised by unstable substrate with many open patches of bare sand in between the vegetation. These patches are ideal opportunities for the establishment of new species (Axmanová et al. 2021). From our field survey, we can conclude that *S. inaequidens* is indeed capable of colonising these open patches. The results from our lab experiment further indicate that establishment of *S. inaequidens* can enhance marram growth in particular, but probably also plant growth in general, after it dies off and nutrients become homogenised. Analogous posi-

tive effects on growth of co-occurring plants have been found for other *Senecio* species (van de Voorde et al. 2011). This enhanced plant growth can lead to an overall shift towards more vegetated dunes, thus further intensifying the worldwide trend towards dune stabilisation (Gao et al. 2020). Dune stabilisation directly implies lower sediment transport to dune parts further inland, which may enable establishment of other species and hence accelerate natural succession.

For marram grass specifically, reduced sediment supply due to dune stabilisation leads to a shift towards a more clustered vegetation configuration (Reijers et al. 2021) which optimises sand capture at small spatial scales (Reijers et al. 2019). In contrast, the potential for dune formation at larger spatial scales will be reduced, affecting dune geomorphology as a whole, ultimately resulting in lower dunes (Reijers et al. 2021). If lowered sediment supply indeed also accelerates dune succession, marram grass will be replaced more rapidly by other plant species less capable of forming dunes.

In conclusion, invasion of dune ecosystems by *S. inaequidens* could lead to a shift in sand dynamics by colonising bare sand patches, in turn accelerating the natural succession of dune vegetation. This could hamper dune growth and further reduce dune height. A reduction in dune height could in turn compromise coastal protection, since higher dunes are known to better protect the hinterland (Zarnetske et al. 2012; Seabloom et al. 2013).

Data availability

The raw data are available via Zenodo at https://doi.org/10.5281/zenodo.6138540. (Van De Walle et al. 2022).

Author contributions

RVDW, MLV and DB designed the lab experiment. RVDW conducted the practical work, analysed the data and wrote the first draft of the manuscript. All authors contributed substantially to interpretation of the results and revision of the manuscript.

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Supplementary material 1

Tables S1, S2, Figures S1, S2

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Data type: docx. file

Explanation note: Occurrence data *Senecio inaequidens*: Table S1. The spatial scale, coefficients, degrees of freedom (df), AICc values and weights for all models. PCA growth experiment: Figure S1. PCA plots for growth experiment. Groups: (left) biota-treatment: red = sterilized, blue = unsterilized; or (right) *Senecio*-treatment: red = *S. inaequidens*, blue = unvegetated sand. Table S2. Correlation of all measured traits with PC1. Sensitivity analysis of result: Figure S2. The analysis of the occurrence data, rerun without samples with very low P and JC values.

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